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A MIDDLE PLEISTOCENE VERTEBRATE FOSSIL ASSEMBLAGE FROM CATHEDRAL CAVE, NARACOORTE, SOUTH AUSTRALIA

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Summary

BROWN, S. P. & WELLS, R. T. (2000). A Middle Pleistocene vertebrate fossil assemblage from Cathedral Cave, Naracoorte, South Australia. *Trans. R. Soc. S. Aust.* **124** (2), 91-104, 30 November, 2000.

Located in the Naracoorte Caves Conservation Park, Cathedral Cave represents one of the more fossil-rich vertebrate sites within the region. An analysis of the geology and palaeontology of the fossil assemblage, coupled with U-series dating, has enabled a reconstruction of both the accumulation modes and the proximal environment between about 280,000 and 160,000 years ago, during the Middle Pleistocene. A pitfall trap is suggested as the primary mechanism for collecting animals whose remains became incorporated in the deposit. The fauna indicates an environment dominated by large herbivores inhabiting a grassy open forest or woodland with little suggestion of aridity.

KEY WORDS: Naracoorte, Cathedral Cave, fossil assemblage, U-series dating, taphonomy, Middle Pleistocene, pitfall trap.

Introduction

The Oligo-Miocene limestone (Naracoorte Member of the Gambier Limestone) underlying much of the Naracoorte region contains an extensive system of caves well known for their fossil content. The best studied are the richly fossiliferous deposits in Victoria Fossil Cave (e.g. Smith 1971, 1972, 1976; Van Tets & Smith 1974; Wells 1975; Tyler 1977; Wells *et al.* 1984). However, little is known about the fossil content of other caves in the region. Ongoing geochronological and palaeontological research (Ayliffe & Veeh 1988; Ayliffe *et al.* 1998; Moriarty *et al.* 2000) has encompassed many 'new' fossiliferous cave sites. The Fossil Chamber in Cathedral Cave is one such site (Fig. 1). The present study presents a detailed geological, taphonomic and faunal analysis of the Cathedral Cave fossil deposit.

Materials and Methods

Geology: stratigraphy and sedimentology

A survey datum was established on a limestone block in close proximity to the sediment cone in the Fossil Chamber (Fig. 2). The sediment fill was systematically probed with a 1 m long 10 mm diameter rod to locate subsurface limestone blocks. A 75 mm diameter soil auger was then used to sample the sediment to a depth of 2 m avoiding the buried blocks. Auger holes were spaced at 5 m intervals across the sediment fill. Each bore hole was sampled at 10 cm increments and a subsurface stratigraphy constructed. All depths to datum were measured. A sample of sediment from each 10 cm interval was placed into a clear snap-lock plastic bag and labelled with the auger hole location and depth. Samples were returned to The Flinders University of South Australia and scored for sediment colour (Munsell colour charts), clay content, calcium carbonate content, grain size and sorting (following the procedures of Day 1965), and grain morphology (McCollough sand gauge).

Palaeontology

Access to the Fossil Chamber was via a dug crawlway approximately 120 m in length (Fig. 1). Excavation of fossiliferous sediments was carried out over a three-month period to April 1998. Two pits were excavated within the Fossil Chamber (Fig. 2). The first (Pit A) measured 2.8 m x 1.5 m x 0.76 m and the second (Pit B) measured 2.6 m x 2.1 m x 1.04 m.

Sediment was carefully excavated along the bedding planes using trowels, dental picks and brushes. Exposed fossils were left *in situ* while the following data were collected: the depth below, distance to, and direction from datum; the dip and bearing of the specimens. A sighting compass, tape measure and a line level were used to accomplish this. Specimens were then removed from the sediments and transported to the laboratory where they were cleaned and stabilised with a polyvinyl butyrate (Mowital®, Hoechst). Due to the difficulty of removing sediment from the cave it was dry screened on site using 5 mm mesh sieves.

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Taphonomic analysis

Each specimen was identified where possible to species or genus and element type. It was then examined for breakage pattern, presence of predator marks, abrasions, weathering and any other noticeable surface modifications (root etching, burning, colour alteration). Breakage patterns were classified as irregular perpendicular, crenulated, spiral and compression following Lyman (1994) and Marshall (1989). Characterisation of weathering stages follows Behrensmeyer (1978).

Following Andrews (1990), all large mammal skeletal elements were counted (Ni) and their relative abundance (Ri) calculated. The relative

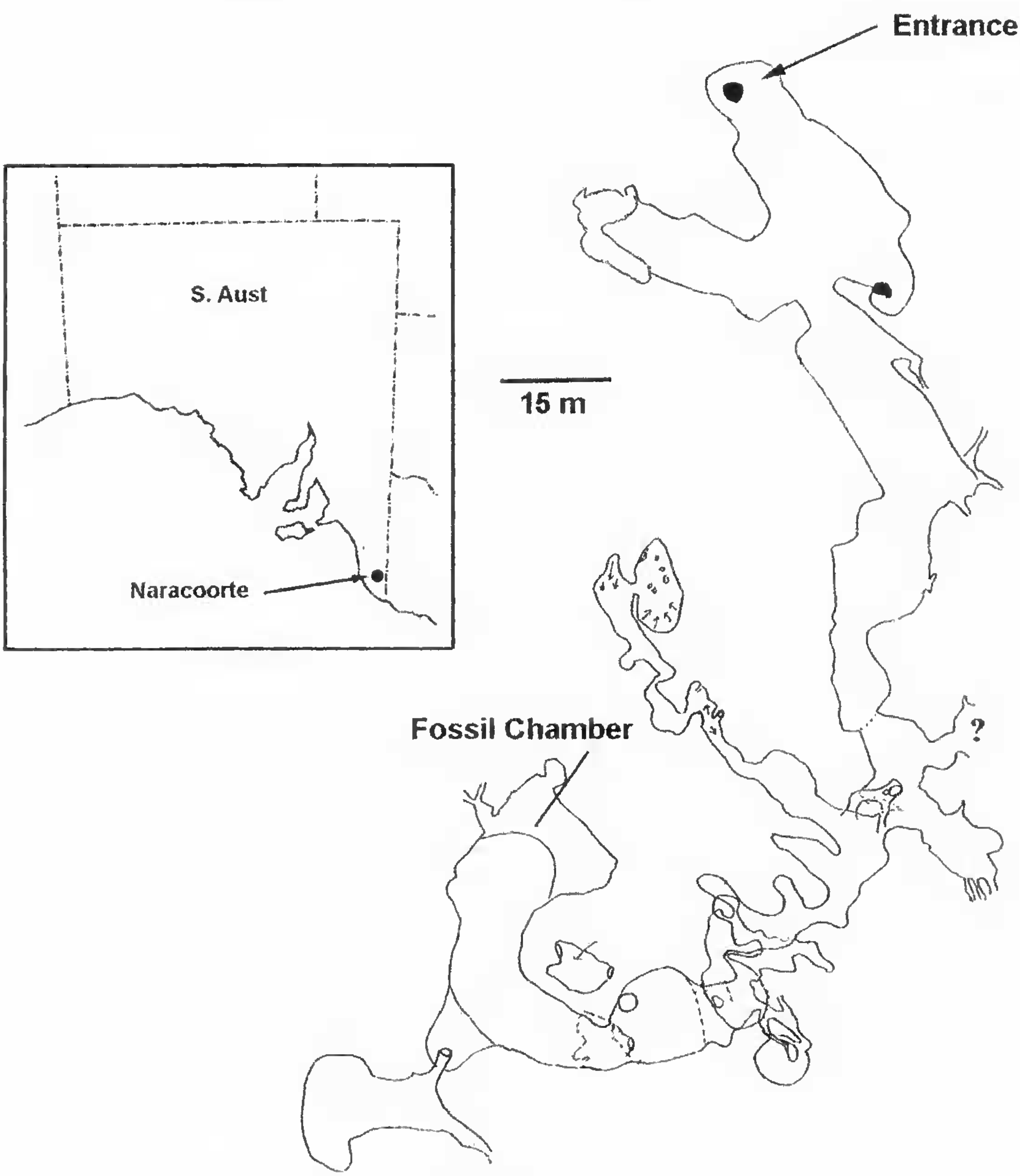

Fig. 1. Map of Cathedral Cave, Naracoorte, showing the position of the study site. Modified from Cave Exploration Group of South Australia surveyed map of Cathedral Cave.

abundance counts were based on the relationship between the Ni, the expected numbers of each element (Ei) within a complete skeleton, and the minimum number of individuals (MNI). This is summarised as:

$$\mathbf{Ri\ \% = \frac{Ni}{(MNI)(Ei)} \times 100}$$

The MNI was produced by summing the most abundant skeletal element referrable to the taxon in question and dividing this by the number represented in a complete skeleton. These results were then totalled to give an overall large mammal MNI. Species MNI were based primarily on the number of craniodental specimens, as these contain the species-specific characters, while MNI values for genera were based on elements, usually post-cranial, which could not be identified to species level. Ei was calculated by multiplying the MNI by the number of each element type present in a complete skeleton. The Red Kangaroo, *Macropus rufus* (Desmavrest, 1922) was used as the comparator skeleton for Ei calculations. To enhance accuracy, caudal vertebrae were excluded from these calculations, as there is considerable variation in the number of tail vertebrae between species.

Results

Cave sediments

Sediments accumulated as a simple cone beneath a solitary roof entrance now choked with sediment, limestone blocks and calcite formation. Within the cone, four sedimentary units were easily identified (designated 1, 2, 3 and 4) on the basis of colour. All units consist of quartz sands with variable quantities of admixed clay (Table 1). Carbonaceous material is abundant in Units 1 and 2, sparse in Unit 3 and absent from Unit 4. Vertebrate fossils were recovered from all units with the exception of Unit 4. Units 1, 2 and 4 are continuous throughout the Fossil Chamber. Unit 3 is restricted to the distal regions of the sediment cone. All sediments have similar characteristics of grain size (Fig. 3) and shape, and clay content. Sediment colour was unique for each unit.

Geochronology

Three U-series dates on calcite deposits interlayered with the fossiliferous sediments in Cathedral Cave were reported by Ayliffe *et al.* (1998). These ages along with an additional date (CC FC FS-4) obtained during this study are presented in Table 2. A small quantity of bone was found deposited within the flowstone layers. All sediment units (1 to 4) lie beneath the flowstone structure (CCFC FS-2) dated at 159.2 ± 2.2 ka. A flowstone (CCFC FS-3) dated at 279.2 ± 7.2 ka lies below Unit 3 while overlying Unit 4. The stratigraphic relationship between the sedimentary units and the dated flowstones is shown in Fig. 2.

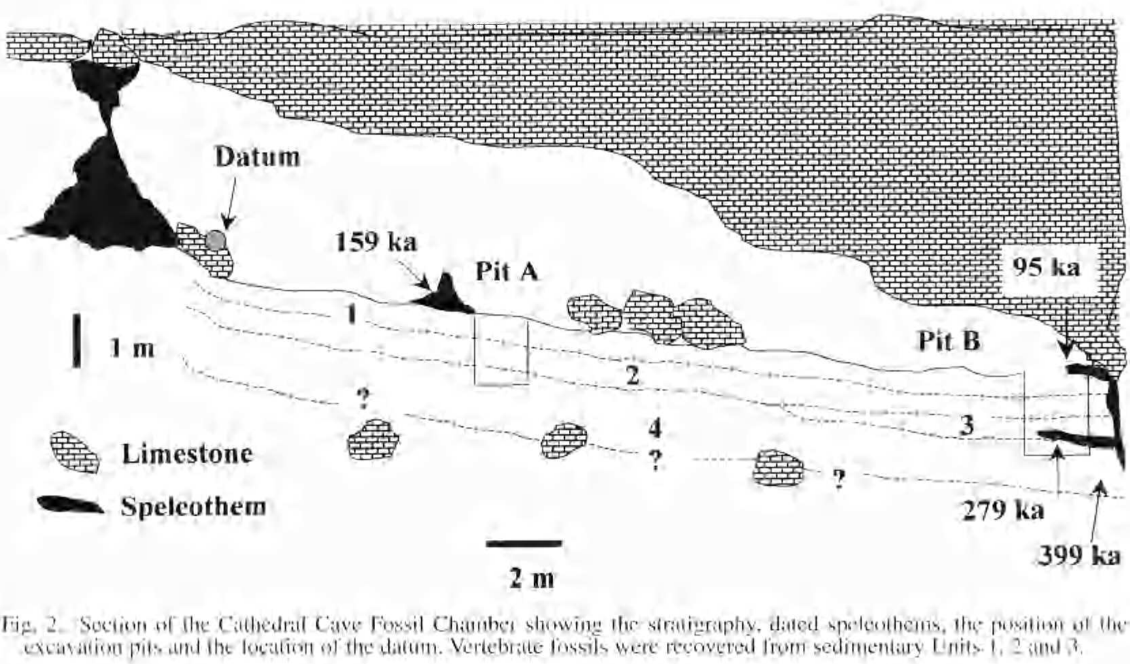

Fig. 2. Section of the Cathedral Cave Fossil Chamber showing the stratigraphy, dated speleothems, the position of the excavation pits and the location of the datum. Vertebrate fossils were recovered from sedimentary Units 1, 2 and 3.

Palaeontology

ASSOCIATION AND ARTICULATION

During excavation it was evident that some bones were either in association or articulation.

All of the associated specimens were from either extinct (*Procoptodon*, *Sthenurus*) or extant (*Macropus*) species of kangaroos. Based on MNI calculations, parts of five (3 *Sthenurus* spp., 1 *Procoptodon* sp. and 1 *Macropus* sp.) individuals were found in association representing 2.8% of the total number of specimens recovered.

Figure 4 shows an articulated specimen *in situ*. Articulated material represented 1.6% of the total number of specimens recovered. Articulated specimens include both extinct (*Sthenurus gilli* Merrilees, 1965, one individual) and extant (*Macropus* sp., one individual) kangaroos and an extant bandicoot (*Isoodon* sp., one individual). The discovery of the articulated partial skeleton of *S. gilli* is the first ever recovered and will be described elsewhere. The articulated bandicoot skeleton was encased within a mass of calcite. The arrangement of its bones was not consistent with an owl pellet.

BREAKAGE PATTERNS

Figure 5 shows the distribution of breakage patterns for the total fossil assemblage.

TABLE 1. *Characteristics of sedimentary units within the Cathedral Cave Fossil Chamber.*

Unit No.	Clay %	$CaCO^3$ %	Sand %	Sediment colour Munsell	Sand colour Munsell	Grain shape
1	8.7	5	86.3	Yellowish red 5YR5/8	Reddish yellow 5YR6/8	SR-SA
2	6.5	7.1	86.4	Dark red 2.5YR4/8	Yellowish red 5YR5/8	SR-SA
3	8.2	3	88.8	Reddish yellow 5YR6/8	Very pale brown 10YR8/2	SR-SA
4	8.9	2.3	88.8	Very pale brown 10YR8/4	Very pale brown 10YR8/3	SR-SA

Sand colour refers to the colour of dry sediment after removal of the clays.
Grain shape: SA = sub-angular; SR = sub-rounded.

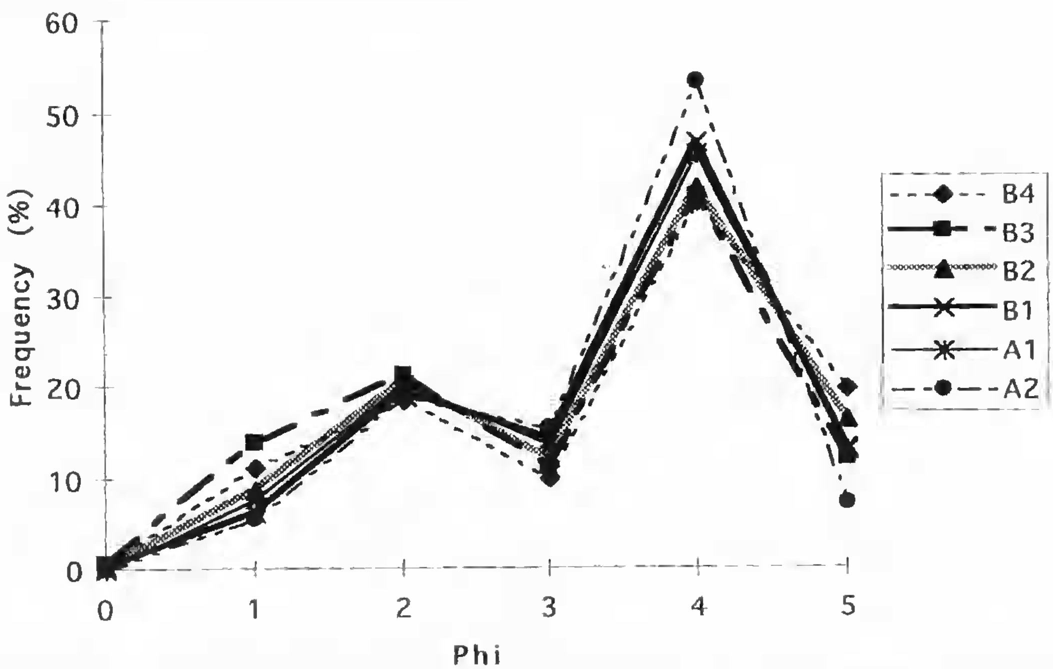

Fig. 3. Grain size distribution of all sediment units from the Cathedral Cave Fossil Chamber. Alphabetical prefixes refer to excavation pit and the sediment unit number follows.

TABLE 2. *Summary of U/Th dates on calcite deposits in Cathedral Cave Fossil Chamber.*

Code number	Date (ka)	Comments
CC FC FS-4	95.2 ± 1.3	Overlies Units 1, 2 and 3, Pit B.
CC FC FS-2	159.2 ± 2.2	Overlying all sedimentary units; provides minimum age of fauna; sediment influx ceases
CC FC FS-3	279.2 ± 7.2	Underlies fossil bearing sediments; gives maximum age for Units 1, 2 and 3
CC FC St-1	399 ± 19	Provides absolute maximum age of fauna

Dates and sample code numbers from Ayliffe *et al.* (1998) and Ayliffe (pers. comm. 1998). Code number abbreviations: CC, Cathedral Cave; FC, Fossil Chamber; FS, flowstone; St, stalactite.

Fig. 4. An example of one of the articulated specimens *in situ* in the Cathedral Cave fossil deposit. This large macropodine vertebral column (cervical to sacral vertebrae) including some pelvic elements, was retrieved intact. Scale bar = 10 cm.

Approximately half of all specimens collected (48%) were entire (i.e. no breakage); another 25% showed evidence of clean recent breakage during excavation and/or removal. The remainder showed breakage patterns of more ancient origin that included irregular perpendicular (22.5%), crenulated (2.3%), spiral fracture (1.4%) and compression (0.8%). The majority of compression fractured specimens were concentrated in the lower Unit 3.

PREDATION AND SCAVENGING

Bone damage caused by predation or scavenging (including surface markings such as puncture wounds and crenulated gnaw damage) was evident on 2.5% of specimens. Predation or scavenging damage was restricted to bones of kangaroos of the genus *Macropus* with an estimated body mass of less than 60 kg. None of the very large extinct marsupial species (e.g. *Zygomaturus*, *Procoptodon*) exhibited predator damage.

SURFACE FEATURES

Few specimens from the Cathedral Cave fossil assemblage showed evidence of burning. Burning is commonly recognised by the carbonisation of the bone collagen, discolouring the bone to black (charring) or producing a chalky white texture from prolonged exposure to high temperatures (calcination) (Brain 1981).

A few long bone fragments had a uniform deep brown surface discoloration that in places penetrated into the cancellous core. Specimens from swamp sites such as Rocky River on Kangaroo Island show similar discoloration.

No evidence of root etchings or abrasions was found on any specimen from the fossil sample. Some 'pseudo-abrasion' patterns were observed (i.e. abraded cancellous bone), but these were interpreted as preparation damage.

Few specimens showed evidence of sub-aerial weathering. Figure 6 shows the frequency distribution of bone weathering with the vast majority of specimens categorised as weathering stage 0.

SKELETAL ELEMENT ABUNDANCES

The skeletal element abundances for large mammals from each fossiliferous sedimentary unit in each pit are presented in Table 3. On average, the relative abundances (mean Ri%) of skeletal elements representing large mammals are between 4.3% and 6.3%. The highest relative abundance values are for mandibles (mean of 19.6%), femora (11.1%) and tibiae (12.4%). The lowest mean relative abundance values obtained are for phalanges (0.7%), carpals (0.6%) and metacarpals (0.2%). Although the absolute numbers of vertebrae and ribs are the highest for most units, their relative abundances are close to the mean.

SPECIES MNI

Tables 4 and 5 show the MNI values for each species identified from the Cathedral Cave fossil

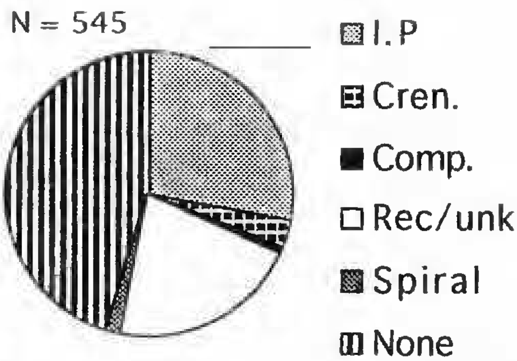

Fig. 5. Distribution of the various breakage patterns observed on the entire Cathedral Cave fossil sample (N = 545). Abbreviations: I. P., irregular perpendicular. Cren., crenulated. Comp., compression. Rec./unk., recent (post depositional) or unknown damage.

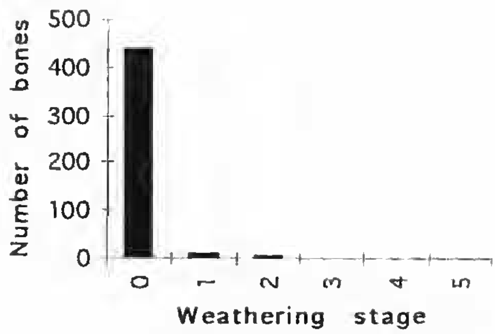

Fig. 6. Frequency distribution of specimens displaying characteristics of the various weathering stages (following Behrensmeyer 1978) from the Cathedral Cave fossil assemblage.

TABLE 3. *Large mammal skeletal element abundance (No.) and relative abundance (Ri%) from both excavation pits and all fossiliferous sedimentary units in the Cathedral Cave Fossil Chamber, Naracoorte.*

Pit	B		B		A		B		A		
Unit	3		2		2		1		1		Mean
Element	No.	Ri%	No.	Ri%	No.	Ri%	No.	Ri%	No.	Ri%	Ri%
Skulls	4	12.1	3	7.5	1	7.7	1	11.1	0	0.0	7.7
Maxillae	4	6.1	11	13.8	1	3.8	1	5.6	0	0.0	5.9
Mandibles	13	19.7	22	27.5	4	15.3	3	16.7	3	18.8	19.6
Individual teeth	9	0.8	6	0.4	13	2.9	0	0.0	5	1.8	1.2
Vertebrae	46	5.2	61	5.6	19	5.4	13	5.3	18	8.3	6.0
Ribs	24	2.8	21	2.0	10	3.0	3	1.3	12	5.8	3.0
Scapulae	4	6.1	1	1.3	0	0.0	1	5.5	1	6.3	3.8
Humeri	3	4.5	4	5.0	1	3.8	1	5.5	1	6.3	5.0
Radii	3	4.5	3	3.8	2	7.7	0	0.0	3	18.8	7.0
Ulnae	1	1.5	4	5.0	1	3.8	2	11.1	1	6.3	5.5
Carpals	0	0.0	0	0.0	1	0.5	0	0.0	3	2.7	0.6
Metacarpals	0	0.0	0	0.0	1	0.8	0	0.0	0	0.0	0.2
Pelvic elements	13	4.9	9	3.8	3	2.9	3	4.2	1	1.6	3.5
Femora	16	24.2	9	11.3	2	7.7	0	0.0	2	12.5	11.1
Tibiae	11	16.7	6	7.5	1	3.8	5	27.8	1	6.3	12.4
Fibulae	2	3.0	1	1.3	1	3.8	2	11.1	1	6.3	5.1
Tarsals	10	2.2	7	1.3	5	2.7	0	0.0	3	2.7	1.8
Metatarsals	13	4.9	16	5.0	5	4.8	0	0.0	1	1.6	3.3
Phalanges	12	0.7	12	0.6	8	1.1	2	0.4	4	0.9	0.7
Totals	188		196		79		37		60		
Mean Ri%		6.3		5.4		4.3		5.6		5.6	

assemblage. A total of 103 large mammal and 107 small vertebrate individuals is represented by the fossil collection. The most common species was the Eastern Grey Kangaroo, *Macropus giganteus* (Shaw, 1789). In total, kangaroos of the sub-family Macropodinae are the most frequently represented species (49.5%), followed by those of the extinct Sthenurinae (37.9%). The most prevalent small mammal species were rodents.

Species abundances

Figure 7 shows the proportions of each large mammal species within the entire fossil sample based on MNI values. Herbivores are represented by 97.1% of all large mammal fossils. Approximately half (51.5%) of herbivores in the deposit are extant kangaroo species of the genera *Macropus* and *Wallabia*. *Macropus* spp. dominate the grazing niche, while the extinct sthenurine kangaroos (37.4%) along with *Wallabia bicolor* (Desmarest, 1804) make up the majority of browsing herbivores. Large carnivores make up only 3% of the total fauna.

Body mass distribution

Figure 8 displays the body mass distribution for large mammals (>5 kg). Body mass estimates were obtained from Calaby (1995), Jones (1995), Lee & Ward (1989), Merchant (1995), Murray (1984, 1991), Poole (1995), Rounsevell & Mooney (1995), Wells (1995) and Wroe *et al.* (1999) using maximum male weights. The large mammal distribution shows a high frequency of individuals weighing between 5 and 20 kg and between 40 and 60 kg. Very few very large individuals (>100 kg) are represented in the fossil deposit.

Mammal habitats

Table 6 shows the preferred or inferred habitats of all the mammal species represented in the Cathedral Cave fossil assemblage. The majority of species inhabited an open forest or woodland environment. Some species are known to occupy a wide range of present day habitats and, consequently, are less informative. *Zygomaturus trilobus* (Macleay, 1858) has been suggested by Murray (1984) to have

Table 4. *Minimum number of individuals (MNI) for large mammals from all fossiliferous sedimentary units, Cathedral Cave, Naracoorte.*

Pit Unit	A 1	A 2	B 1	B 2	B 3
Thylacinus cynocephalus				1	
Total Thylacinidae MNI				1	
Lasiorhinus latifrons		1			1
Vombatidae Indet.			1		1
Total Vombatidae MNI		1	1		2
Macropus giganteus	2	3	4	10	1
Macropus rufogriseus		1		2	5
Macropus sp. Indet.	1	3	1	10	6
Wallabia bicolor					2
Total Macropodinae MNI	3	7	5	22	14
Sthenurus gilli	1	1		5	5
Sthenurus brownei	1	1		2	1
Sthenurus occidentalis				2	1
Sthenurus sp. Indet.	2	2	2	5	6
Procoptodon goliah				1	1
Total Sthenurinae MNI	4	4	2	15	14
Zygomaturus trilobus	1	1	1	1	1
Total Zygomaturinae MNI	1	1	1	1	1
Thylacoleo carnifex				1	1
Total Thylacoleonidae MNI				1	1
Total No. extinct species	4	4	2	8	8
Total No. extant species	2	4	3	3	5
Total No. species	6	8	5	11	13
Total MNI extinct species	5	5	3	18	17
Total MNI extant species	3	8	6	22	16
Total MNI	8	13	9	40	33

N.B. *Sarcophilus harrisii* is present in the assemblage but was recovered during a previous excavation and the stratigraphic origin is unknown.

inhabited wetlands, such as swamps or billabongs and its diet may have included vegetation growing along the banks of water holes.

Discussion

Geology

Cathedral Cave lies within the Naracoorte East Dune which contains a series of potential sediment sources for cave fills, including Pleistocene beach-dune, estuarine-lagoonal and lacustrine facies, and Pliocene marine and fluviolucastrine facies (Cook *et al.* 1977; Grimes 1994). These sandy facies, individually or in a combination, are a likely source for the Cathedral Cave sediments, although soil formation, leaching and/or mixing makes it difficult to establish firmly sediment provenance.

The sedimentary units within the Fossil Chamber appear to be continuous between excavation pits with the exception of Unit 3. No distinction between sedimentary

TABLE 5. *Minimum number of individuals (MNI) for small mammals, reptiles, amphibians and birds from all fossiliferous sedimentary units, Cathedral Cave, Naracoorte. Indeterminate family or class individuals were not included in total extinct/extant species calculations.*

Pit Unit	A 1	A 2	B 1	B 2	B 3
Sminthopsis murina		1			
Antechinus flavipes			1		
Antechinus sp. Indet.		1		1	
Phascogale calura		1	1	1	
Dasyurus viverrinus	1	1			
Dasyurus maculatus			1		
Total Dasyuridae MNI	1	4	3	2	
Perameles bougainville	3		1		
Perameles gunnii	2	2		1	
Perameles sp. Indet.	6	1	1	3	
Peramelidae Indet	3	5		1	1
Total Peramelidae MNI	15	8	2	4	1
Cercartetus nanus		1			
Total Phalangeridae MNI		1			
Bettongia penicillata	1	1		1	
Potorous platyops	2			2	1
Potorous tridactylus					1
Bettongia sp. Indet.		1		1	
Total Potoroidae MNI	3	2		4	2
Mastacomys fuscus	8	3	4	5	1
Pseudomys australis	5	1		8	
Pseudomys shortridgi	1				
Notomys mitchelli		1		2	
Pseudomys sp.	2				
Total Muridae MNI	16	5	4	14	1
Aves Indet.	3	1	3		1
Total Aves MNI	3	1	3		1
Tiliqua rugosa	2	1		1	
Total Reptilia MNI	2	1		1	
Limnodynastes sp. Indet.	2	1			
Total Leptodactylidae MNI	2	1			
Total No. extinct species	1	0	0	1	1
Total No. extant species	21	14	6	10	2
Total No. species	22	14	6	11	3
Total MNI extinct species	2	0	2	1	
Total MNI extant species	36	17	9	23	3
Total MNI	42	23	12	25	5

BROWN, S. P. (1998) A Geological and Palaeontological Examination of the late Pleistocene Cathedral Cave Fossil Accumulation, Naracoorte, South Australia. BSc (Hons) Thesis, The Flinders University of South Australia (unpub.).

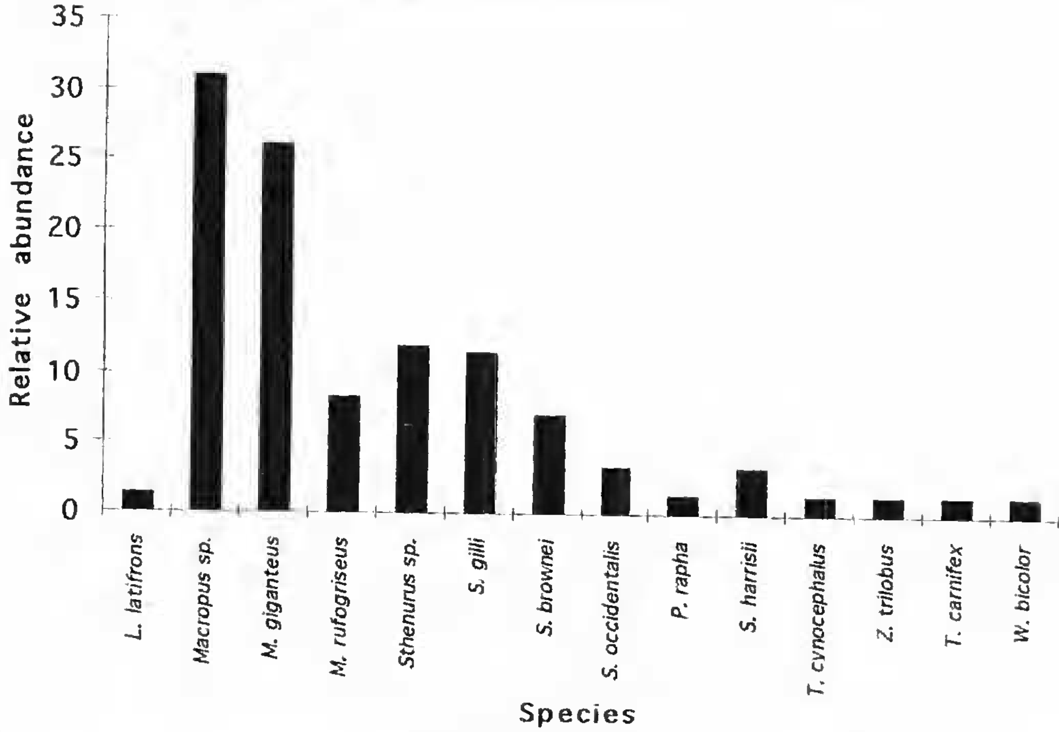

Fig. 7. Frequency of the number of individuals of the various large mammal species expressed as percentages of the total number of individuals from the Cathedral Cave fossil assemblage.

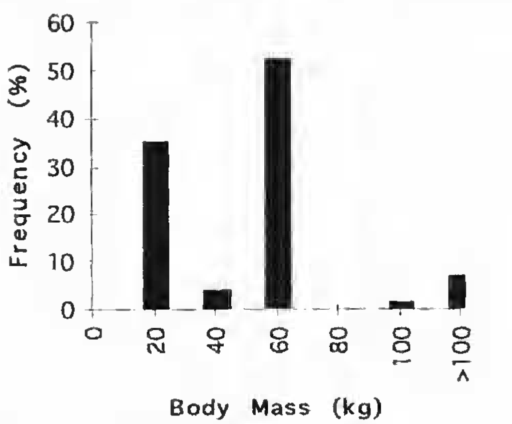

Fig. 8. Distribution of all large mammal species based on MNI values plotted by weight classes from the Cathedral Cave fossil assemblage.

units could be made based upon the grain size distribution or grain shape. Calcium carbonate and clay content varied between the sedimentary units with little similarity with the sediments of the region (Brown 1998[1]). The variation in calcium carbonate content of the cave sediments may have occurred following incorporation of cave limestone via fretting from the Fossil Chamber roof (Wells *et al.* 1984). Pleistocene beach-dune facies are prevalent in the region but are not interpreted as the source for the Cathedral Cave sediments due to their very high amount of calcium carbonate content. Moriarty *et al.* (2000) suggested that the cave fills at Naracoorte were sourced from surface soils during periods with a wet climate regime with abundant vegetation (i.e. interglacials, stadials and interstadials). However, Units 3 and 4 contain little or no carbonaceous material suggesting that surface soil development may not be significant during the deposition of these units and they may have originated during more arid periods where rainfall and vegetation cover were low.

The speleothem dates provide a time frame and suggest environmental conditions under which sediment accumulated within the Fossil Chamber. The buried flowstone (CC FC FS-3) gives a maximum age (279.2 ± 7.2 ka) for sediment and fauna accumulation in Units 1, 2 and 3 and a minimum age for the underlying Unit 4 sediments.

A U-series date from near the lower end of the buried stalactite (399 ± 19 ka) provides a maximum age for Unit 4, as burial of this speleothem had to occur following its formation.

The speleothem developed on the upper surface of the sediment cone, dated at 159.2 ± 2.2 ka, provides a minimum date for cessation of sediment deposition

TABLE 6. *Preferred or inferred habitats of mammal species recovered from the Cathedral Cave fossil assemblage, Naracoorte.*

Species	F	S	H	O. F.	W	R
Antechinus flavipes			X	X	X	X
Sminthopsis murina			X	X	X	X
Dasyurus viverrinus		X	X	X		
Dasyurus maculatus			X	X	X	
Sarcophilus harrisii			X	X	X	
Thylacinus cynocephalus		X		X	X	
Phascogale calura				X		
Isoodon obesulus			X	X	X	
Perameles bougainville			X	X	X	
Perameles gunnii		X	X	X		
Bettongia penicillata		X	X	X	X	
Potorous platyops				X	X	
Potorous tridactylus			X	X	X	
Lasiorhinus latifrons		X				
Macropus giganteus		X		X	X	
Macropus rufogriseus			X	X	X	
Wallabia bicolor		X	X	X	X	
Sthenurus gilli				X		
Sthenurus brownei				X		
Sthenurus occidentalis				X		
Procoptodon goliah		X		X		
Cercartetus nanus				X	X	X
Zygomaturus trilobus				X	X	
Thylacoleo carnifex				X	X	
Mastacomys fuscus			X	X	X	X
Pseudomys australis	X	X				
Pseudomys shortridgi			X			
Notomys mitchelli				X		

Data obtained from Archer (1981), Bradley (1995), Christensen (1995), Edgar & Belcher (1995), Fox (1989, 1995), Friend & Burbidge (1995), Godsell (1995), Happold (1995), Heinsohn (1966), Jarman and Phillips (1989), Johnston (1995), Murray (1984), Seeback *et al.* (1989), Tate (1947), Turner & Ward (1995), Walton (1988), Watts & Aslin (1981) and Wells (1995). F = Forbs, S = Savannah, H = Heath, O.F. = Open forest, W = Woodland and R = Rainforest.

in the chamber, which probably occurred following blockage of the solution tube entry point. In other words, the entire Cathedral Cave fauna from Units 1, 2 and 3 dates between 279.2 ± 7.2 and 159.2 ± 2.2 ka corresponding with oxygen isotope stages 6, 7 and 8 (Shackleton & Opdyke 1973; Martinson *et al.* 1987).

Taphonomy

ACCUMULATION MODE(S)

The fossil evidence supports accumulation of animals via a pitfall trap. The low number of mammalian carnivores and the scarcity of carnivore tooth markings and gnaw damage (characterised by crenulated breakage patterns), suggest that the fossils were not accumulated by mammalian carnivores and the chamber was not used as a den or a lair (cf. Lundelius 1966; Sutcliffe 1970; Brain 1980; Haynes 1980; Scott & Klein 1981; Cruz-Uribe & Klein 1994; Skinner *et al.* 1998). Furthermore, the absence of root etching and the small number of burnt or sub-aerial weathered bones argue against a surface accumulation where animal remains would be easily accessible to carnivores. The few specimens displaying characteristics of carnivore activity were most likely hydraulically transported into the cave from locations proximal to the entrance or resulted from an entrapped carnivore within the chamber.

Although water transport of animal remains into the Fossil Chamber may account for some post-mortem damage, the aforementioned evidence suggests that bone accumulation did not occur by this means. All evidence is consistent with a pitfall trap.

The deep brown discoloration of some bones seems to contrast with the paler colours typical of the deposit. The deep brown specimens are comparable to bones found in swamp deposits at Rocky River on Kangaroo Island (Wells *et al.* 1999) where the colour has been attributed to tannin uptake or staining. Perhaps this type of surface colouring present on some Cathedral Cave specimens indicates local ponding within the cave system at a time when outside conditions of high vegetation cover increased the quantity of tannins into the downward percolating ground water.

The data obtained for the small vertebrate fauna (Table 5) suggest at least two modes of accumulation. The low total number of individuals and the small number of arboreal species are not inconsistent with a pitfall trap. Arboreal species would be more able to climb out of the cave had they fallen or climbed in. However, the higher number of rodent individuals recovered from Pit A, Unit 1 and Pit B, Unit 2 suggests that an avian predator may have roosted within the cave or solution tube or in an overhanging tree. One might infer from the relatively small number of individuals compared with other extensive owl deposits at Naracoorte (McDowell 2000[1]) that this only occurred for a short time.

ARTICULATED SPECIMENS

The presence of articulated fossil specimens suggests that some animals entered the cave intact. These were presumably live animals, trapped by the pitfall mechanism, which either died from the fall into the cave and decomposed on the cone or survived the fall and were subsequently able to move about within the chamber. As the majority of articulated material was recovered from the distal fan regions within the Fossil Chamber, the latter scenario seems the more likely. Observations by one of the authors (RTW) of contemporary accumulations suggest that following entrapment, starving animals became thigmotaxic and tended to seek out the security of walls and crevices and died there. This evidence further supports the hypothesis that a pitfall mechanism was the primary mode of accumulation for large mammals and indicates that the burial of some bones occurred rapidly before disarticulation could occur.

The lack of articulated material representing very large mammals (>100 kg) (i.e. *Procoptodon* sp. and *Zygomaturus* sp.) suggests that either their remains were transported into the cave or the diameter of the solution tube acted as a 'body mass sieve', preventing the passage of larger, intact animals. As already discussed above, the absence of weathering, abrasions from hydraulic transport and any extensive bone surface discoloration suggests that the bones did not accumulate outside the cave. The size of individuals of these species may have prevented their falling directly into the chamber below. The individuals would be trapped and then die within the solution tube, with their remains gradually incorporated into the fossil deposit as the carcasses decomposed. The low MNI values for these large herbivore species suggest one or all three possibilities; that few became trapped, that they could readily extricate themselves, that their numbers were low in the immediate vicinity of the pitfall.

SKELETAL ELEMENT ABUNDANCES

The skeletal element abundances for each unit and excavation pit indicate that the relative number of skeletal elements recovered (Ri%) is low. Accepting the hypothesis of a pitfall mechanism capturing live animals at random, the majority of bone in the deposit would result from decomposition of whole or near whole animals within the Fossil Chamber. In this case, an individual's entire skeleton should be represented within the total fossil deposit and so would give high Ri% values were the entire deposit to be sampled. The low observed relative abundances are thus interpreted as an artefact of sampling. These values also indicate dispersal of elements following accumulation under transport regimes such as sediment mass movement, water flow and/or bioturbation.

Palaeontology

COMPARISON WITH VICTORIA FOSSIL CAVE

Victoria Fossil Cave, located about 700 m from Cathedral Cave, contains several fossil sites that have yielded an array of Middle Pleistocene faunas, though only the main Fossil Chamber has been thoroughly researched (Wells *et al.* 1984; Moriarty *et al.* 2000). The Fossil Chamber assemblage is by far the largest and richest in all the caves at Naracoorte (Wells *et al.* 1984). Fossil-rich sediments appear to have been deposited prior to 213 ka and span many thousands of years (Ayliffe *et al.* 1998; Moriarty *et al.* 2000). A pitfall trap is suggested to be the primary mechanism responsible for the accumulation of animals (Wells *et al.* 1984). A majority of the more common megafaunal species also occurs within Cathedral Cave (e.g. *Sthenurus gilli*, *S. brownei* Merrilees, 1967, *S. occidentalis* Glauert, 1910 and *Zygomaturus trilobus*). The major faunal differences between the two assemblages lie in the presence of the rarer species in Victoria Fossil Cave (e.g. *Palorchestes azael* Owen, 1873, *S. andersoni* Marcus, 1962, *S. maddocki* Wells & Murray, 1979, *S. pales* DeVis, 1895, *Sthenurus* sp. nov., *S. baileyi* Prideaux & Wells, 1998 and *Protemnodon roechus*

[1] McDowell, M. C. (2000) The small mammals and sediments of Robertson Cave, World Heritage Naracoorte Caves Conservation Park, South Australia. Abstract of poster presented at the Quaternary Studies Meeting. Regional analysis of Australian quaternary studies: strengths, gaps and future directions, Canberra 7-9 February 2000 (unpubl.)

Owen, 1874) and are likely to reflect differences in sample size.

Preliminary faunal samples have been obtained from dated deposits in Spring Chamber and Grant Hall within Victoria Fossil Cave (Moriarty *et al.* 2000). Many species detected in the Cathedral Cave fossil assemblage were not recovered from Spring Chamber. This may be an artefact of the small sample size from Spring Chamber. U-series dates obtained indicate that the Spring Chamber fauna is older than that of Cathedral Cave (Ayliffe *et al.* 1998; Moriarty *et al.* 2000), although some overlap occurs during the period 282-211 ka corresponding to the upper portion of the Cathedral Cave date range (279-159 ka).

Grant Hall sediments appear to have a higher fossil content than those of Spring Chamber and the fauna is more like that of Cathedral Cave. The megafauna represented closely resembles the Cathedral Cave fossil assemblage. Moriarty *et al.* (2000) suggested an age between 160 and 80 ka for sediment accumulation in Grant Hall. However, they argue that this may not be the true age of the sediment influx and fauna due to the potential for reworking of previously deposited sediments.

PROXIMAL COMMUNITY AND PALAEOENVIRONMENTAL RECONSTRUCTION

An understanding of the taphonomic biases within the fossil assemblage gives more confidence to any palaeoenvironmental reconstruction, but, as the fauna accumulated during a period of approximately 120 ka, time-averaging may compromise this interpretation.

It can be concluded that the large mammal component of the proximal community consisted primarily of herbivores. Of these, grazing types (*Macropus* spp.) were the most abundant. The browsing herbivore fauna consisted of the extinct sthenurine kangaroos, *Wallabia bicolor* and *Zygomaturus trilobus*. Vegetation allowing this mix of herbivores to coexist within the same region would include shrubs, trees and grasses. An open forest or woodland with a grassy understorey is the most likely environment. However, grazing kangaroos could also forage in more open areas within a forest, on the forest edge or adjacent grasslands. Murray (1984) suggested that the morphology of the *Zygomaturus* nasals may be an adaptation for browsing on reeds within shallow water, suggesting the possible presence of wetlands or swamps.

The presence of *Lasiorhinus latifrons* (Owen, 1845) in the deposit appears inconsistent with this environmental reconstruction. Today, this species inhabits semi-arid to arid savannah regions (Wells 1995). However, in the Mid-Pleistocene, this species may have inhabited the outer edge of open forest or woodland, as even in historic times its range extended into higher rainfall areas (Wood-Jones 1924).

Most of the small animal fauna is indicative of an open forest/woodland environment. A smaller number occurs today in savannah and heath vegetation suggesting it may have occurred in close proximity to Cathedral Cave during the Middle Pleistocene.

Medium-sized mammals such as bandicoots (*Perameles* and *Isoodon*) need sufficient ground cover for refuge and the presence of low-lying scrub is suggested. *Antechinus flavipes* (Waterhouse, 1838), *Phascogale calura* (Gould, 1844) and *Cercartetus nanus* (Desmarest, 1818) are arboreal species. This further supports the presence of abundant trees consistent with an open forest/woodland. The only arid species recovered from the fossil deposit was the Plains Rat, *Pseudomys australis* (Gray, 1832) which Walton (1988) suggests prefer today rocky arid regions.

The fauna suggests a vegetation structure similar to that of the region prior to European land clearing. Croft *et al.* (1999) indicate that the vegetation community of the Naracoorte region was dominated by open eucalypt forest/woodlands with intermittent tussock grasslands and sedgeland prior to European settlement. The diversity in vegetation for the region during the Middle Pleistocene as indicated by the Cathedral Cave fossil fauna suggests that on a local scale the vegetation may have been ecotonal.

PALAEOCLIMATE

During the period bracketing the Cathedral Cave fossil assemblage (between 159 and 279 ka) a glacial maximum occurred at 270 ka along with an interglacial (oxygen isotope stage 7e) and warm interstadial periods centred on 240, 220 and 195 ka (Ayliffe *et al.* 1998; Winograd *et al.* 1997). Martinson *et al.* (1987) reported three radiolarian high temperature peaks for the Southern Ocean (RC11-120) during the time of faunal accumulation at 240, 220 and 195 ka with a maximum temperature of about 0.5 °C higher than present and lowest temperatures averaging 3 °C below present. The high temperature peaks correlate with the interglacial or warm interstadial events of this period. Ayliffe *et al.* (1998) suggest speleothem deposition followed these phases corresponding to stadials and cool interstadials. Little bone accumulated during periods of speleothem formation suggesting that the majority of animal remains were accumulated during the warmer interglacials and interstadials. Accepting this hypothesis enables the dates for the span during which the faunal remains were accumulating to be refined to the period 240 ka to 195 ka.

Ayliffe *et al.* (1998) indicated that the regional hydrological balance at present is an analogue for interglacial conditions, and taking this into account it is concluded that the majority of animal remains accumulated during periods of local climate similar to that of the present time.

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